PROC. R. SOC. VICT. vol. 98, no. 3, 121-131, September 1986

THE IMPACT OF SEVERE FROST ON MALLEE EUCALYPTS, *BANKSIA ORNATA* AND *LEPTOSPERMUM CORIACEUM* AT WYPERFELD NATIONAL PARK

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Abstract: The severe frosts of 1982, perhaps interacting with the ensuing drought, had dramatic immediate effects on *B. ornata, L. coriaceum* and the mallee eucalypts. Except for sporadic survivors, all adult *B. ornata* in frost-affected swales were eliminated. Seed from frost-affected cones shows poor germination, even after subsequent fire. *L. coriaceum* showed high and variable kills of standing foliage, but the population is recovering from coppice and suckers, even in the worst-affected areas. Mallee eucalypts responded to frost damage by coppicing in a pattern related to the severity of the damage. Very few seedlings established in the frost-killed areas, the majority of which lie in bare ground outside the litter layer.

In June and July of 1982, very severe frosts were experienced in parts of Wyperfeld National Park (Table 1). Although periods of winter frost are common in this region, nothing of this severity has been recorded since detailed climatic records were initiated in 1959 at the Ranger's residence. Data for Ouyen, which date back to the early 1900s, suggest that frosts of this severity may be very rare occurrences. The 1982 frost was accompanied by a severe drought, the worst since 1959. The annual rainfall (108 mm) was only 30% of the annual average (351 mm) and the rainfall data collected at the Ranger's residence show that from July 1982 to February 1983, no month had more than 10 mm and the total precipitation was only 30.5 mm (Table 2). Data for Rainbow show 1982 as the lowest rainfall since records began in 1901, again with only 29 mm in the same period.

The impact on the vegetation was dramatic. Thousands of hectares of mallee scrub and heathland were devastated, especially in the interdune swales. Adult *Banksia ornata* and *Leptospermum coriaceum* were severely affected in the heathlands, while *Eucalyptus incrassata, E. dumosa* and *E. foecunda* showed distinctive effects in the scrublands. Areas rich in these species were selected for detailed study in 1985.

Preliminary investigations showed that frost-killed banksias failed to regenerate by coppicing. Very few seedlings were encountered in these areas and the majority of follicles on the cones of frost-killed bushes remained closed. Healthy flowering banksias were found on dune crests and occasionally as survivors in swales. Since the majority of frost-affected banksias were dead it was decided to evaluate the status of the seed reserves held in the frost affected cones and to study the response of leaves of *Banksia* to an experimental freezing treatment.

Stands of frost-affected *L. coriaceum* showed many adults had been killed. Many plants were coppicing from the base of dead stems, or producing suckers from lateral roots. In many cases, this coppice regrowth was itself dead or dying. Seedlings were infrequent. It was decided to assess the impact of freezing on seeds in capsules of *L. coriaceum*, the impact of experimental freezing on adult and seedling foliage, and the severity of frost-induced injury at field sites.

Frost-affected mallee eucalypts showed typical coppice regrowth: death of adults was rare. Severely-

Table 1
Minimum Temperatures (°C: Screen Data) Wyperfeld Ranger's Residence

	JUNE 1982						JULY 1982							
Date	4	5	6	7	8	9	15	16	17	18	19	20	21	22
Temperature	−5.0	−8.0	−8.0	−7.0	−6.0	−5.0	−1.0	−5.0	−7.0	−1.0	+3.0	−6.0	−8.0	−6.0

Table 2
Monthly Rainfall Records (mm) Wyperfeld Ranger's Residence

	J	F	M	A	M	J	J	A	S	O	N	D	TOTAL
1982	14.6	13.5	12.0	12.0	14.4	17.3	4.3	9.9	5.2	2.1	1.2	2.0	108.5
1983	5.8	0	99.5	21.7	35.0	21.2	35.4	59.8	53.6	57.4	21.1	55.0	465.5

affected trees, in which the whole of the canopy had been destroyed, coppiced mainly from the lignotuber; less severely-affected trees coppiced along the length of the stems. Seedlings were rare. It was decided to evaluate the impact of experimental freezing treatments on seed viability in the capsule and when shed, and the distribution and number of seedlings beneath frosted eucalypts.

METHODS

Seed Collection

Capsules of *Leptospermum* were collected from healthy, apparently unfrosted plants on the upper slopes of Eastern Lookout and Flagstaff Hill (Fig. 1). Green and brown capsules occurred on those bushes, green capsules being the products of the last flowering period, brown capsules being from earlier flowering periods. Seed was extracted by allowing capsules to open at room temperature in paper bags and then rubbing opened capsules firmly between the palms of the hand. Seeds were separated from chaff.

Cones of *Banksia* were collected along Nine Mile Square Track, either from adults killed by frost or from undamaged bushes flowering at the time. Seed was released by heating cones in an oven at 200°C for 1 hour or by setting fire to cones on a BBQ grill and removing them as follicles opened and before the seeds were lost.

Capsules of *E. incrassata* were collected from Eastern Lookout, *E. dumosa* from the Lowan Track and *E. foecunda* from the Dattuck Track (Fig. 1), in all cases from long unburnt and unfrosted stands. Seed was extracted by placing capsules in an oven at 30°C for 2-3 days; chaff was separated from seed.

Seed Germination and Seed Viability

All attempts to germinate seeds of *B. ornata* and *L. coriaceum* on filter paper, with or without surface sterilization, were unsuccessful. Two artificial, sterilized soil mixes gave highly variable results. Accordingly, viability was estimated by placing seeds sliced through the embryo in 0.1% tetrazolium violet in phosphate buffer at pH 6.8 in the dark for 45 minutes. Viable embryos turn red (Moore 1973).

The seeds of all three eucalypt species were germinable on filter paper. Seeds were germinated in sets of 100 (5×20 per dish) held at 25°C in a 12 hour light/dark cycle, for 40 days at $60 \mu E\ m^{-2}\ sec^{-1}$ (Grolux fluorescents). Germinated seeds were removed every 2-3 days. This method yielded high results for *E. incrassata* (93% germination) and *E. dumosa* (99%) but gave variable results (58%, 33%, 77%) with *E. foecunda*. *E. foecunda* gave high results (94%) when germinated in the same manner but at uncontrolled room temperatures in fluctuating light conditions. Preliminary trials with *E. incrassata* showed no differences between seeds from younger and older capsules. Tests on *E. incrassata* and *E. dumosa* showed no significant differences between seed lots from different trees (*E. incrassata*, 7 trees: *E. dumosa*, 3 trees), so pooled seed samples were used throughout.

Simulated Frost Treatments

Seed and Capsules

Capsules of *L. coriaceum* were divided into three groups: one was used as a control, one group was frozen once and the third group twice over two days at −20°C for 8 hours. This experiment was repeated six times. 50 seeds per treatment were assessed for viability.

Unopened eucalypt capsules or seeds extracted from capsules were given one of three treatments: 1×4 hours, 1×28 hours or 7×4 hours, each at −20°C. Seed was extracted from frozen capsules in the normal manner. This experiment was repeated on dry and imbibed seeds (an imbibition curve for *E. incrassata* established that imbibition was complete in 30 minutes). One additional experiment was carried out on *E. incrassata* only. One hundred seeds, germinated until seed coat rupture, were exposed to 2×4 hours at −20°C with 20 hours between freezing treatments.

Vegetation

A portable, battery-operated fridge/freezer (ENGEL model MRFT 56.0-A4) was used to freeze either isolated shoots of *B. ornata* and *L. coriaceum* or attached branches (*L. coriaceum* only) in the period July 16-23, 1985.

Branches from each of two tagged adult *B. ornata*, one from the dune top the other a survivor in a dune swale, were collected from Nine Mile Square Track, as were seedlings that had germinated after the 1981/82 fire. Two kinds of control were used. For the adults, fresh leaves were collected daily from the tagged bushes. For the seedlings, shoots were maintained in water after the initial harvest, and fresh leaves from these shoots were measured each day. Treated plants were frozen at −20°C for 8 hours each day for 7 successive days. After removal from the freezer, the bottom 3 cm was cut from the base of each shoot under water to prevent xylem blockage. After a 2-hour thawing period, five leaves were sampled from each treatment and control. Several dozen hand sections were prepared, pooled and stained for about 2 min in 5% Evans Blue (Gaff & Okong'O-Ogola 1971). Ten sections were assessed by light microscopy for percentage cell death (dead cells stain blue, live cells remain unstained), the mean of the ten calculated and plotted as mean per cent cell death against time.

Three types of adult foliage were chosen for *L. coriaceum*: branches from a mature healthy plant (termed "stem"); healthy basal coppice regrowth (termed "basal") and healthy root-sucker coppice (termed "root-sucker"). These parts were collected separately from dune crest and dune swale. Seedling shoots were also collected from the swale as none were found on the dune crests. All these shoots were treated and maintained, controls established and percentage cell death measured as described for *B. ornata*.

A part of two mature *L. coriaceum* plants was also frozen in the field. The portable freezer was placed beside the plant, a few mature shoots were bent over into the freezer and the lid closed and fastened. The

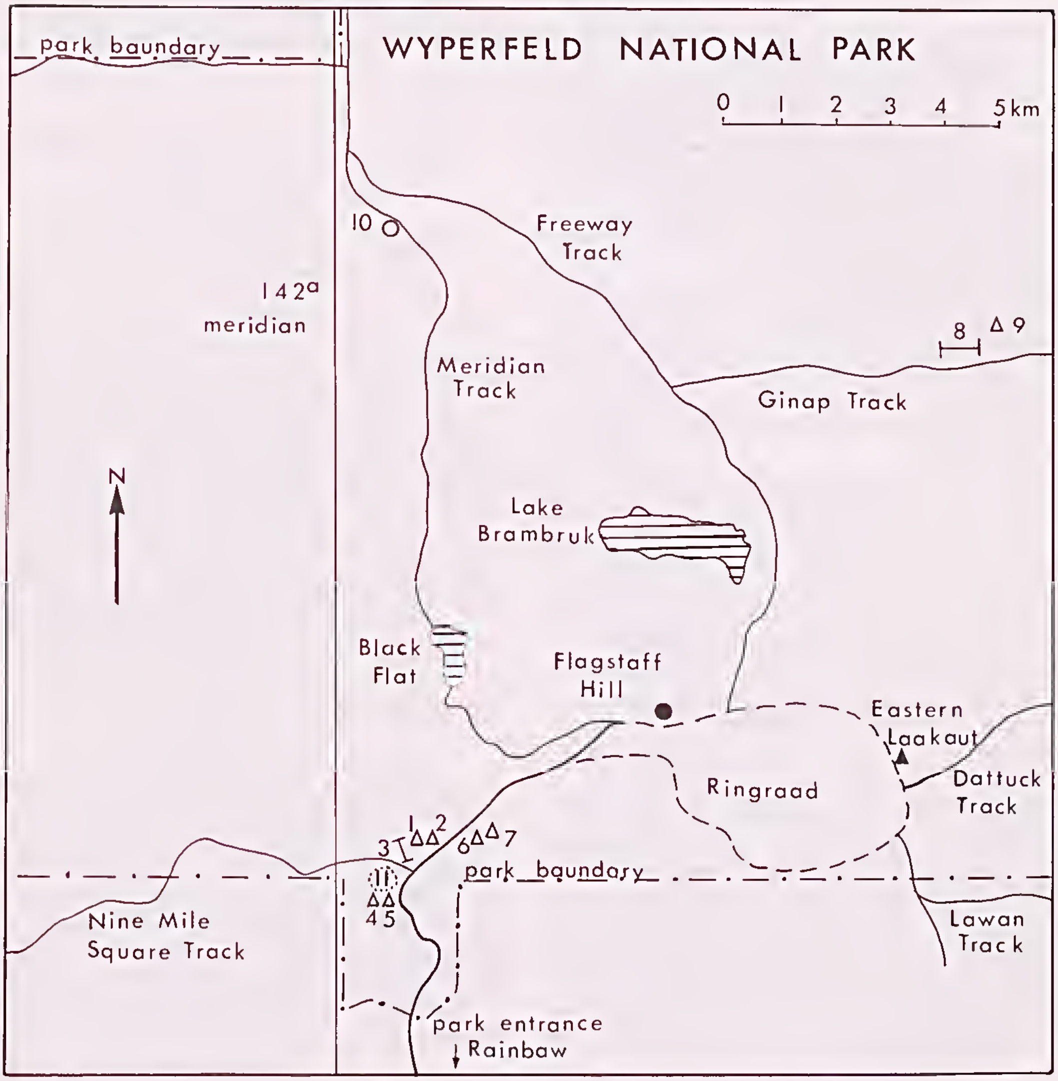


Fig. 1—Map of part of Wyperfeld National Park showing tracks and study sites. △ *L. coriaceum* sites assessed for post-frost regrowth |–| Transects used to study seedlings induced by frost (site 3), and induced by fire in January 1981 (site 8). ○ Frost-killed *B. ornata* site, burnt by fire in January 1985. ...... Area used to measure frequency of seedling eucalypts beneath eucalypts showing various degrees of frost damage.

shoots were given a single treatment of 8 hours at −20°C. One of the plants had green, closed capsules on its frozen branches.

Field Measurements

Basal and Root Sucker Regrowth Assessments of L. coriaceum

This experiment was designed to measure the condition of the basal and root-sucker coppice regrowth of *L. coriaceum* in different areas. Basal regrowth is coppice occurring from the bottom of otherwise dead parent stems, and root sucker regrowth arises from horizontal roots.

Seven sites, all showing extensive frost damage, were chosen, four at Nine Mile Square Track (Sites 1, 2, 4, 5, Fig. 1), one along Ginap Track (Site 9, Fig. 1) and two at a dune 4.5 km along the entrance road from the main gate (Sites 6, 7, Fig. 1). In each site, 176 plants were assessed with the percentage death of the frost-induced coppice regrowth for each plant being recorded. Some plants had no coppice regrowth on the main stems and appeared to be dead: these are recorded as "basal coppice absent". The condition of 176 root suckers was recorded in the same areas. Because open capsules were observed on frosted *Leptospermum*, seedlings were counted in a 30 m × 30 m quadrat placed at random within the sites used for the coppice regrowth assessments. Though most suckers were multi-stemmed, the seedling nature of these plants was confirmed by partial excavation.

Frost-Induced Eucalypt Seedlings

A 400 m belt transect, marked every 10 m, was set out near Nine Mile Square Track (Site 3, Fig. 1). The transect began on a dune crest in an *E. incrassata* stand, and ended in an *E. foecunda* stand in a swale. Eucalypt seedlings were counted within 1 m either side of the transect line. The initial recordings were made in February 1985 and each seedling was marked by placing a coloured tag next to it. The fate of the marked seedlings was recorded finally in August 1985.

A second belt transect, 600 m long, also marked every 10 m, was set out adjacent to the Ginap Track (Site 8, Fig. 1). Part of this transect, from the 0-370 m mark, was burnt in the summer of 1981/82, before the area was exposed to the severe frosts of 1982. Again, all seedlings within 1 m of either side of the transect were recorded and marked.

In an attempt to measure the impact of frost severity on the abundance of seedlings beneath frosted trees, a frost severity scale was constructed arbitrarily as follows:

A. Severe frost: no canopy present, regrowth from lignotuber only.
B. Medium frost: no canopy, coppice regrowth from stems and lignotuber.
C. Light frost: some canopy present, stem coppice only.
D. Very light frost: nearly all canopy present, little coppice evident.

Trees with seedlings beneath them were assessed for frost severity (Site 11, Fig. 1). Next, the distribution of seedlings in relation to the tree was measured as follows. The tree was taken to be in the centre of two circles: the radius of the first gave the area covered by litter fall. The radius of the second circle minus that of the first allowed calculation of the litter-free zone beyond the litter layer in which most seedlings seemed to occur. Trees without seedlings were not measured because, in the case of the severely-frosted categories, it was not possible to be sure that the trees had capsules on them before the frost.

RESULTS

Viability of Seeds in Cones of *B. ornata*

The data are set out in Table 3.

Table 3
Percentage Seed Viability in 3 replicate trials (100 Seeds/Trial): *B. ornata.*

Cone Opening Technique	Cone Type			
	Frosted	Mean	Unfrosted	Mean
Oven	74, 70, 69	71	79, 83, 85	82
Firing	85, 82, 86	84	90, 97, 86	91

A two way ANOVA was conducted using a BMDP2V program after arcsine transformation of the data. The result showed highly significant differences between the frosted and unfrosted cones ($P<0.001$) and the technique used to open them ($P<0.005$).

Viability of Seeds of *L. coriaceum*

The data are set out in Table 4.

After arcsine transformation, an ANOVA was carried out which showed highly significant effects of site and treatment ($P\leq 0.01$) and no significant effect of capsule colour. The first-order interaction of site × capsule colour was also highly significant ($P\leq 0.01$). Since sites showed significant effects and capsule colour did not, SNK tests were done on the treatment means after pooling results across colours. Because sites were significant, the SNK test was done separately for Eastern Lookout and Flagstaff Hill. The result is shown in Table 5. Means

Table 4
Percentage Seed Viability for *L. coriaceum* Treatments*

Treatment	Location							
	Eastern Lookout				Flagstaff Hill			
	Replicates	Mean	±	sd.	Replicates	Mean	±	sd.
Control, Green[1]	88,73,80,84,94,68	81.2	±	9.6	62,53,60,56,73,57	59.2	±	8.1
Control, Brown[2]	58,79,62,77,66,68	68.3	±	8.3	60,65,60,67,74,70	66.0	±	5.5
Frosted × 1[3], Green	64,64,65,66,64,68	65.2	±	1.6	50,44,51,40,57,41	47.2	±	6.6
Frosted × 1, Brown	56,68,55,73,58,63	62.6	±	7.2	48,58,46,56,49,58	52.3	±	5.4
Frosted × 2[4], Green	62,60,59,58,53,53	57.5	±	3.7	41,46,43,40,38,37	40.8	±	3.3
Frosted × 2, Brown	26,64,32,59,40,49	45	±	15.0	40,54,42,52,43,55	47.7	±	6.7

* 50 seeds measured per replicate.
1. Seed extracted from green capsules.
2. Seed extracted from brown capsules.
3. Capsules frosted for one 8-hr period at −20°C.
4. Capsules frosted twice for 8 hrs at −20°C, with 20 hrs at room temperature.

underlined are not significantly different from one another ($P > 0.05$): all other means from each site are significantly different ($P \leq 0.01$).

TABLE 5
SNK TESTS ON SEED VIABILITY OF *L. coriaceum* (DATA FROM TABLE 4)

	Arcsine of % Viability		
Site	Control	Frosted Once	Frosted Twice
Eastern Lookout	60.4	53.0	45.7
Flagstaff Hill	52.7	44.9	41.7

The SNKs show clearly that all freezing treatments reduce viability with respect to controls. However, the viability of seed frozen in capsules from Eastern Lookout is affected more by two freezing treatments than by one, but this is not true for seed from capsules from Flagstaff Hill. There, even though the mean viability is reduced by two freezing treatments, there is no significant effect of the second treatment.

FREEZING TREATMENTS ON CAPSULES OF *Eucalyptus*

The results are set out in Table 6.

TABLE 6
PERCENTAGE GERMINATION OF SEEDS* EXTRACTED FROM FROZEN CAPSULES

Species	Unfrozen Capsules	Frozen Capsules Frost Treatment		
		1×4 hr	1×28 hr	7×4 hr
E. incrassata	99	93	80	87
E. dumosa	99	91	71	82
E. foecunda	94	88	90	97

* 100 seeds measured per treatment

FREEZING TREATMENTS ON DRY AND IMBIBED SEEDS OF *Eucalyptus*

The results are set out in Table 7.

TABLE 7
PERCENTAGE GERMINATION OF SEEDS* FROZEN EITHER DRY OR IMBIBED †

Species	Unfrozen Seed	Frozen Seed					
		1×4 hr		1×28 hr		7×4 hr	
		Dry	Imbibed	Dry	Imbibed	Dry	Imbibed
E. incrassata	99	98	97	98	97	95	37
E. dumosa	99	91	92	85	98	94	30
E. foecunda	94	85	98	88	90	94	63

* 100 seeds measured per treatment.
† All seeds imbibed for 30 minutes prior to first freezing treatment.

Although the results shown in Tables 6 and 7 were not replicated, the results are very clear cut: the only treatment to reduce seed germinability is 7×4 hr treatments imposed on imbibed seeds (Table 7). In seeking an explanation of this phenomenon, and of the difference between *E. foecunda* and the other two species, it was noted that germination was proceeding during the 7 days over which the 7×4 hr treatments were administered and that *E. foecunda* was the slowest species to germinate. It seems likely that the high death rate in the 7×4 hr imbibed treatments was due to the onset of germination in the sample during the treatment period. To confirm that germinated seeds were frost sensitive, one hundred germinated seeds of *E. incrassata* were given 2×4 hr freezing treatments with a 20 hr period at room temperature between them: all seeds were killed by this treatment.

SIMULATED FROST TREATMENTS GIVEN TO VEGETATION

The results for *B. ornata* foliage are shown in Fig. 2. Adult foliage began to show rapid death after 5 repeated freezing treatments, and the source of the foliage (dune crest or swale) was without effect. Seedling foliage remained unaffected throughout the treatment period.

The results for *L. coriaceum* are set out in Figs. 3-5. The contrast with *Banksia* is quite striking. All adult tissues show significant cell death after just two freezing treatments, with tissues from swale plants being slightly more sensitive than those taken from dune crests. Interestingly, tissues from root sucker coppice take longer to die than other sources of adult foliage, independent of site. As Fig. 5 shows, seedling tissue has about the same sensitivity as adult foliage (dune crest seedlings were not available to test).

The parts of the plants frozen in the field had turned brown 4 days after exposure to the freezing treatment, producing dead branches on an otherwise healthy bush. The green capsules which were frozen on these bushes also opened after 4 days and released their seed.

RECOVERY OF FROSTED *L. coriaceum* IN THE FIELD

The data are shown in Table 8. Plants showing no regrowth are marked as "basal coppice absent".

After arcsine transformation, ANOVA's showed significant differences between sites for the death of both basal coppice regrowth and root sucker regrowth (plants without any basal regrowth were omitted from the ANOVA). Inspection of Table 8 shows clearly that most of the differences between sites are being generated by the observations at sites 5 and 6, which are markedly different from the other five sites. The percentage of plants showing no basal regrowth also shows marked site to site variation, and again it is sites 5 and 6 which lie at extremes of the range.

FROST INDUCED EUCALYPT SEEDLINGS

Results from the Belt Transects

Only 6 seedlings (3 of *E. foecunda* and 3 of *E. incrassata*) were encountered in the 400 m of belt transect through the frosted area at Nine Mile Square Track, and

TABLE 8

PROPORTIONS OF COPPICE PLANTS OF *L. coriaceum* SHOWING VARYING DEGREES OF SUBSEQUENT DEATH AT EACH OF SEVEN SITES[4].

% of Regrowth Shoots Dead		% of Plants at Each Site (*n* = 176)							Mean
		1	2	3	4	5	6	7	
1. Basal Coppice[1]	0	49.4	46.0	38.6	53.4	18.2	7.4	42.6	36.5
	1–25	16.5	30.1	8.5	5.1	79.5	2.3	31.3	24.8
	26–50	6.3	5.7	5.1	3.4	1.1	1.7	0	3.3
	51–75	0	0	0.6	0.6	0	0	0	0.2
	76–100	4.5	4.5	8	1.1	0.6	6.3	0.6	3.7
Basal Coppice Absent[2]		23.3	13.6	39.2	36.4	0.6	82.4	25.6	31.6
2. Root Sucker Coppice[3]	0	65.3	70.5	71.6	80.1	48.3	55.7	83.0	67.8
	1–25	28.4	25.0	19.3	16.5	50.0	36.4	16.5	27.4
	26–50	3.4	2.8	2.8	2.3	0	5.7	0.6	2.5
	51–75	0	1.1	0	0	0	0	0	0.2
	76–100	2.8	0.6	6.3	1.1	1.7	2.3	0	2.1

1. Regrowth from base of main stem.
2. No regrowth off main stems, which appear to be completely dead.
3. Regrowth from horizontal roots.
4. All sites are in areas of severe frost kill where the only surviving foliage[5] is from coppice shoots (see Fig. 1).
5. Seedling counts in the same sites (30 m × 30 m quadrat) were 0, 0, 1, 44, 5, 0, 16.

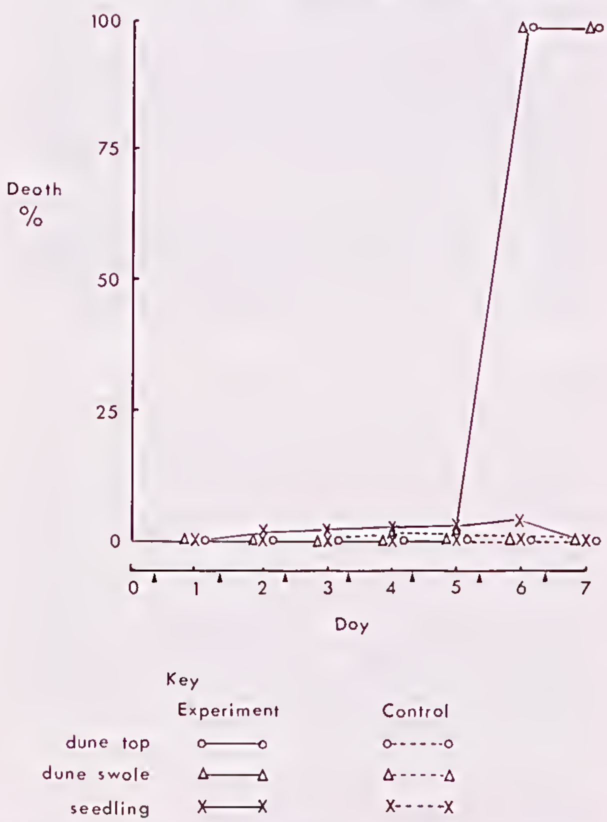


Fig. 2—Percentage of dead cells in leaf tissues of adult and seedling *B. ornata*, following successive freezing treatments at −20°C. The freezing treatments were given at the arrows.

only 4 of these survived till August of 1985 (all still alive 18/2/86).

At Ginap Track, 200 m of the belt transect passed through a patch of vegetation burnt in the summer of 1981/82. This region had 169 seedlings (all *E. foecunda*) that are all the result of the fire (no plant tops survived the fire to act as a seed source during the frost periods). Unfortunately, it is not known precisely when those seedlings germinated. They may be the survivors of germinants induced by the regular low monthly rainfalls from January 1982-June 1982 (average of 14 mm/month: see Table 2). Alternatively, they may not have germinated till the autumn of 1983, following the drought-breaking rains (99.5 mm) of March 1983. Of the 169 seedlings present on 21/2/1985, 158 were still alive at 4/8/1985 (122 at 18/2/1986). The significance of these points is brought out in the discussion.

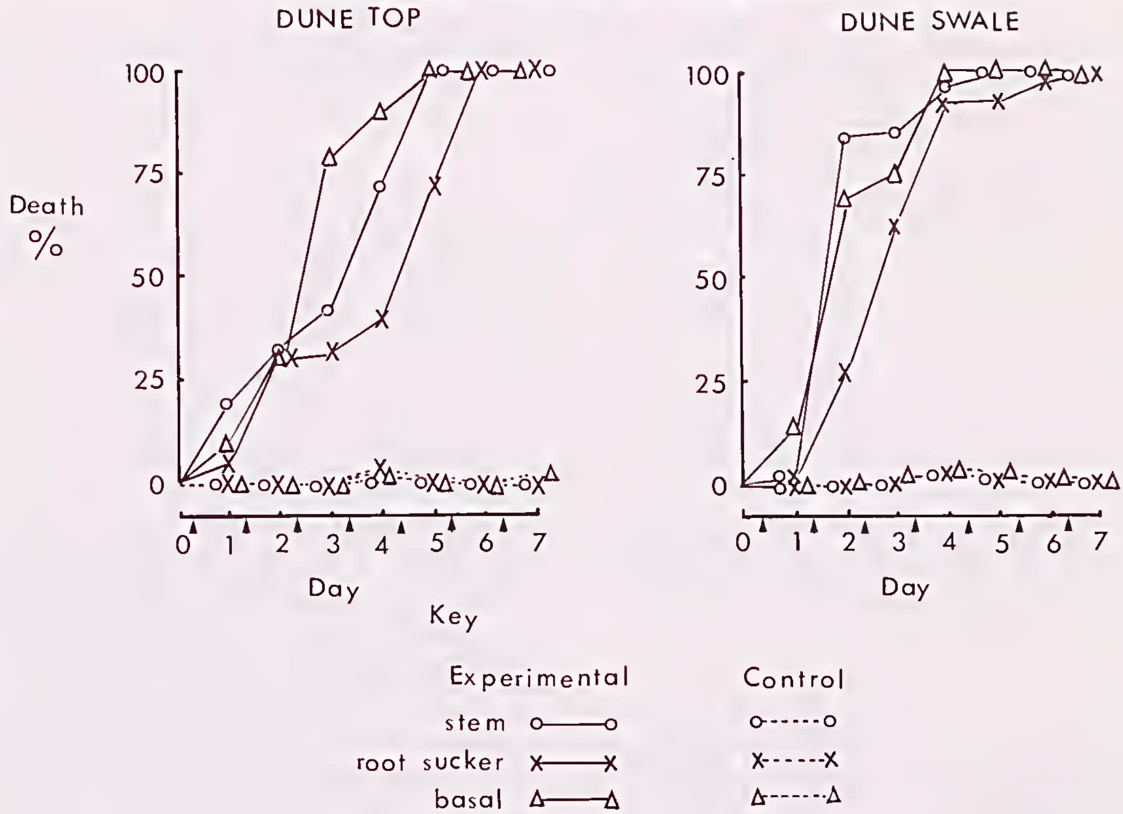
Distribution of Seedlings Beneath Frost Affected Trees

The results are set out in Table 9. All observations were made in an area near to the location of the belt transect at Nine Mile Square Track (Site 11, Fig. 1).

Clearly, all of the seedlings were found in the unlittered areas outside of the litter layer. The number of seedlings per square metre does not vary in any regular manner with the degree of frost damage experienced by the putative parental tree.

DISCUSSION

1982 saw two unusual climatic events impact upon Wyperfeld National Park. Two extended periods of severe frost with screen temperatures dropping to −8°C



Figs 3-5—Percentage cell death induced by successive freezing treatments at −20°C on leaf tissues of *L. coriaceum*. Three types of adult foliage were used: leaves from an undamaged mature plant ("stem"); leaves from healthy basal coppice regrowth ("basal"); leaves from healthy root-sucker coppice ("root-sucker"). Figs. 3 and 4 show the effects on leaves taken from dune top (Fig. 3) and dune swale (Fig. 4). Fig. 5 shows the results from seedlings from the swale (none were available to test from dune tops). Freezing treatments were given at the arrows.

occurred in June and July, and were followed by the worst drought since 1959 (see Tables 1 and 2) and probably the worst since 1901 if data for Rainbow are typical of the area. Unfortunately, temperatures in the dune swales were never measured during that period and such severe conditions did not occur during the 1985 study period. The factors that generated this frost are not known, and are being examined, but it is clear from the patterns of vegetation kill and the local topography that it was not a simple matter of cold-air drainage and the local radiation effects. Anecdotal comments suggest that the temperatures in the swales may have been well below those measured in the screen at the Ranger's residence. For this reason, the temperature of −20°C was chosen to represent the worst imaginable conditions in this situation. It is also impossible to be sure how much influence the subsequent drought had on the effect of the frost. As the boundary between the killed vegetation and healthy vegetation is often very sharp, especially on dune slopes, and because there are often similar sharp

TABLE 9

DISTRIBUTION OF SEEDLINGS IN LITTER-RICH AREA AND UNLITTERED AREA BENEATH TREES SHOWING DIFFERENT DEGREES OF FROST DAMAGE (NINE MILE SQUARE TRACK)

Frost Severity Rating	No. of Trees Sampled	Litter Area (m^2)	Seedling Number	Unlittered Area	Seedling Number	Seedlings/ m^2
			E. incrassata			
A	6	133.2	0	108.6	46	0.42
B	5	85.5	0	54.7	8	0.15
C	10	149.6	0	185.0	17	0.09
D	6	112.5	0	76.1	12	0.16
			E. foecunda			
A	4	72.9	0	97.7	22	0.23
B	4	62.8	0	70.3	33	0.47
C	4	18.9	0	25.7	5	0.19

boundaries within the canopy of a single tree, we incline to the view that most of the damage was done by the frost. The impact on *B. ornata, L. coriaceum* and the mallee eucalypts is discussed separately.

B. ornata

In many parts of the Park, the only surviving adult specimens are now located on dune crests and upper dune slopes above the level affected by the frosts. Large areas of seedlings established after the 1981 fires, still exist in the west of the Park along Nine Mile Square Track. Frost-killed adults failed to coppice: there are occasional adult survivors in the swales, due probably to local vagaries of frost intensity. In fact, as Fig. 2 shows, adult foliage of this species appears to be remarkably resistant to repeated freezing and thawing, even at the very low temperature of −20°C, chosen deliberately to represent the worst state that might have obtained in the swales. Five cycles of freezing and thawing were necessary before a sudden collapse of the tissue occurred. Tissues from the swale survivor did not behave differently from those of the plant from the dune crest. In agreement with field observations, seedling tissues were even more resistant (see Fig. 2), surviving 7 successive freeze/thaw cycles at −20°C. These observations help to understand how *B. ornata* survives in this frost-prone environment.

Wyperfeld normally experiences 5-15 frost days per year but in 1982, this number was 35, including the two severe periods of about a week each shown in Table 1. Presumably, the exceptional winter was more than this normally frost-hardy plant could tolerate. The basis of the resistance of this species to frost is not known. Layton and Parsons (1972) showed that consecutive 6 hr frosts to −5°C would kill 50% of 10 week old *B. ornata* seedlings that were raised in a growth cabinet. Field-grown plants seem to be much more resistant. Scanning electron microscopy confirms that a rich indumentum of coiled hairs is present on the leaves of the adult plant, and is even more strongly developed on seedlings (unpublished observation). Thomas and Barber (1974) showed that leaves of *E. urnigera* would supercool to −10°C if their surface was kept dry, but only to −4°C if the surface was wet. Harwood (1980, 1981), working with subalpine *E. pauciflora*, supported this observation; wetted leaves showed about 16% more leaf damage than unsprayed leaves ($P<0.01$). In those experiments, leaves began to freeze in the range −2.2°C to −6.9°C. While it is possible that the presence of hairs may modify the leaf surface microclimate and modify the effects of freezing, it is, at first sight, hard to believe that such features could allow supercooling to −20°C, the temperatures used in our experiments. However, Lindnow *et al.* (1982) have shown dramatic effects on the temperature at which leaves will freeze depending upon the presence or absence of ice-nucleating bacteria on the leaf surface. Thus, barley leaves with surfaces contaminated by *Pseudomonas syringae*, show 50% frozen cells at −3.0°C; the same tissues taken from plants raised axenically in sterilized nutrient solutions in the absence of these bacteria required −16°C to produce the same effect. Such dramatic effects raise very interesting possibilities for desert plants and need careful evaluation with these species. Paton (1972) has shown that in *E. viminalis*, frost resistance involves more than one mechanism. In a more recent study (Paton 1981) he can find no effect of glaucousness on frost resistance in populations segregating for this character.

Cheal *et al.* (1979) list *B. ornata* as an obligate seed regenerator. Thus the fate of the *B. ornata* in the frost-killed areas clearly hinges now on its seed reserves. The state of these seed reserves is open to question. Though seed from frosted cones has a reasonably high viability in the tetrazolium test, seed from frosted cones has a significantly lower viability (84% vs 91%) than seed from unfrosted cones. More importantly, none of the seed from frosted cones would germinate. Mr A. Salkin (personal communication) says that seed germinability declines rapidly with age in this species. Certainly, thorough searches of frosted stands show very few seedlings and at site 10, where fire in 1985 burnt a large area of previously frosted *B. ornata*, seedling abundance is extremely low (4 seedlings in a 4500 m^2 fixed quadrat, the survivors at April 1986 of 6 recorded in February 1986). Normally, *B. ornata* regenerates strongly after a fire (Gill 1976, 1981). It appears that the frost may induce a catastrophic reduction in the area occupied by *B. ornata* in the Park.

L. coriaceum

As Table 8 shows, of the 1232 plants counted, on average 31% were killed completely. This judgement is based on the failure of these stems to produce basal coppice in the 3 years that have elapsed since the frosts. Furthermore, about 5% of these stems were checked for signs of living bark at ground level; none was detected. An average of 60% of the plants had basal coppice showing less than 25% dieback. This species also suckers freely from its horizontal roots; stands therefore consist of groups of individuals produced initially from seedlings, each of which may have produced clones, by suckering, to an extent that has not been measured. No attempt was made to estimate the proportions of individuals attached to common root systems since preliminary excavations showed that these clones can extend over hundreds of square metres. Similarly, it is not known if suckering is affected by the degree of damage to the above-ground shoot system. Thus, we do not know if plants that failed to generate basal coppice have produced suckers which have survived, even though the "parent bush" is dead to ground level. Root suckers are abundant at all sites and their coppice is very healthy: on average, 94% of such suckers show less than 25% dieback (see Table 8). An interesting feature of these observations is the high between-site variation in the pattern of response. Sites 5 and 6 show extraordinarily low and high (respectively) proportions of dead adults: the same two sites show the lowest levels of undamaged root-sucker coppice. We have made no attempt to explore the sources of this between-site variability but will not be surprised if it is related to variations in soil moisture stresses (see Adams 1985).

The cause of the coppice dieback is likewise unexplained. Dead coppice shoots were often covered with a population of black dots which have been kindly identified by Mr I. Pascoe of the Victorian Plant Research Institute at Burnley Gardens as *Seimatosporium leptospermi*. Bagnall and Sheridan (1972) observed this fungus on *L. scoparium* in New Zealand and on *L. juniperinum* at Bayswater, Victoria. This is the first report of its occurrence on *L. coriaceum*, but no attempt has been made to test its pathogenicity.

Thus, despite the loss of many above-ground shoots and the death from unknown causes of a significant number of the frost-induced coppice shoots, the vegetative regenerative potential of this species appears to be intact, though some sites, (e.g. site 6) lost the majority of their adult shoots.

Footnote 5 of Table 8 notes that seedling numbers in 900 m² quadrats in each site were low and variable. Cheal *et al.* (1979) state that the immediate post-fire responses of this species are unclear, but list the plant as a facultative root resprouter. Specht (1981) states that seedling regeneration in heath vegetation in southern Australia is limited to the period immediately after fire and again when gaps begin to occur in the mature and senescent phases 25 to 50 years post-fire. His data show that the closely-related coastal teatree, *L. laevigatum*, consisted entirely of a population of seedlings at Wilson's Promontory. Unpublished observations in other areas of Wyperfeld regenerating after fires in 1977 suggest that seedlings are an important source of post-fire regeneration in this species. Unlike the eucalypts, seed viability of this species does appear to be affected by severe freezing treatments (see Tables 4 and 5). The results are complex and hard to interpret. Thus, at Eastern Lookout, seeds from green capsules give a higher result in all treatments than seeds from brown capsules, whereas the reverse is true for seeds from capsules from Flagstaff Hill. This produced the unusual result that overall, capsule colour showed no significant effects, but did show a highly significant interaction with locality. Locality also affected the impact of a second freezing period. Seed extracted from capsules at Eastern Lookout showed an extra reduction in mean viability with a second freezing treatment while that from Flagstaff Hill, which has a significantly lower viability after the first treatment, does not show the same response. Further study of multiple-freezing treatments is needed to evaluate the effects of successive treatments for this species.

The intact plants frozen in the field had turned brown and shed seeds from frozen capsules 4 days after the treatment. Given this rapid response, it seems likely that severe frosts would have induced a fairly massive seed release in this species. Even if a majority of seeds were rendered inviable, the low and variable numbers of seedlings re-establishing in the frosted areas seems too low to be due to the impact of frost *per se*. It will be most interesting to assess the belt transect installed in February 1985 at Meridian Track in an area severely frosted in 1982 and then burnt in January 1985. As with the *B. ornata*, such an area will give an interesting comparison with areas re-establishing after fires that were not preceded by frosts.

The Mallee Eucalypts

After a fire, coppice shoots arise chiefly from the lignotuber as it is rare for above ground foliage to survive (Cheal *et al.* 1979). After the 1982 frost, these species also produced coppice but in a pattern that reflected the severity of the frost kill. Severely-affected trees died back to or close to ground level and coppiced from the basal stem or lignotuber, while less severely-affected trees coppiced along the length of the aerial stems.

Very few seedlings were found along the belt transect at Nine Mile Square Track, dramatically fewer (6 vs 169) than those induced by the fire of 1981 along half the length of transect at Ginap Track. Seedling frequency is not consistently related to the degree of frost severity of the parent tree (see Table 9), though those data confirm the low seedling frequency found in the belt transect. It was thought at first that the frosts may have killed seeds within the capsules, but the data of Table 6 and 7 show that this is highly unlikely: dry seeds exposed to 7 successive cycles at $-20°C$, are quite resistant—only germinated seed is susceptible.

Wellington (1984) and Wellington and Noble (1985a, b) have shown that the establishment of seedlings in long unburnt stands of *E. incrassata* is limited by ant predation of the low rate of seed input, and by adult competition for nutrients and water. After fire there is a dramatic increase in the rate of seed input, and sharp reduction in the competitive power of the adults, especially for water. Between them, these factors lead to the establishment of high numbers of seedlings in the early years after a fire. If it is assumed that frozen capsules open in the field (capsules removed from trees and experimentally frozen and thawed opened in a few days at 30°C), one would expect a massive seed release in severely frosted areas, a period of reduced adult competition, and the establishment of a large population of seedlings. Unfortunately, measurements were made only at Nine Mile Square Track and did not begin till early in 1985, two and a half years after the frosts, so it is not possible to be sure exactly what happened immediately after the frosts. However, casual observations were made in August 1983 and August 1984 in several locations in the Park and large seedling populations were never sighted in frost-killed areas. Perhaps seed release, after frost kill in winter, does not generate the sudden massive seed input that follows fires in summer and the ants are able to harvest most of the frost-induced seed fall. Although other interpretations are possible, the total absence of seedlings from the litter layer around frost-damaged trees (see Table 9) could be interpreted to support this view in that chance burial of seed by wind-movement of sand or passing animals might be easier in the litter-free zone. Alternatively, frost-induced litter may have an inhibitory effect upon germination or establishment of mallee eucalypt seeds. With difficulty, it would be possible to test some of these points by using the portable freezer to freeze small samples of eucalypts in the field. Certainly, the conditions surrounding the establishment of seed after a severe winter frost and a prolonged drought are likely to be different from those after summer fires followed by autumn rains.

CONCLUSIONS

The severe frosts of 1982, perhaps interacting with the ensuing drought, had dramatic immediate effects on *B. ornata, L. coriaceum* and the mallee eucalypts. With the exception of sporadic survivors, all adult *B. ornata* in frost-affected swales were eliminated. Field-grown seedling *B. ornata* appears to be highly resistant both in areas exposed to field frost, and when tissues were tested by very severe experimental freezing treatments. The seed in the cones in the frost-killed areas is still viable, based on the tetrazolium test, but it is not germinable and seedlings are rare in frost-killed areas at present (latest observations April 1986). Fire in 1985 burnt a large stand of frost-killed *Banksia* near Meridian Track (site 10, Fig. 1), but this area has regenerated very few seedlings also (less than 1 survivor/1000 m² in a large fixed quadrat of 4500 m²).

L. coriaceum showed high and variable kills of standing foliage, but even in areas that showed 100% loss of leaves and up to 80% loss of mature stems, the population is recovering by coppicing and suckering. Seedling regeneration is weak and variable with site and there is some evidence that seed of this species may be damaged in the capsules by repeated exposure to severe freezing temperatures.

The mallee eucalypts respond to frost damage by coppicing, in a pattern related to the severity of the damage. Only a very small number of seedlings have established in the frost-killed areas, the majority of which lie in bare ground outside the litter layer.

We conclude that *B. ornata* has suffered serious damage from the winter of 1982 and the ensuing drought. Such severe conditions may provide a limitation to the distribution of *B. ornata* over long periods of time, similar perhaps to the influences of frost on distributions of eucalypts in subalpine Tasmania reported by Davidson and Reid (1985). *L. coriaceum* and the mallee eucalypts are recovering strongly.

ACKNOWLEDGEMENTS

The Ministry of Conservation, Forests and Lands provided a Travel Grant without which this work could not have been done. It is a pleasure to thank Mr Arnis Heislers, Mr Peter Muller (Chief Ranger) and his staff at Wyperfeld for their considerable assistance during the course of this study, and Dr R. Parsons for helpful comments on the manuscript. Ms Georgina James kindly typed the manuscript and Dr Paul Boon gave invaluable help with the ANOVAs. The assistance of Dr C. A. Anderson in the early stages of this project is gratefully acknowledged.

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